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## ORAL BREATHING VALVES OF TELEOSTS, THEIR MODIFICATIONS AND RELATION TO THE SHAPE OF THE MOUTH.

EVELYN GROESBEECK MITCHELL.

ALTHOUGH the oral breathing valves of teleost fishes are very prominent and their function important, they have, strangely enough, been almost wholly neglected. Owen ('66), suggests that they "seem intended to prevent the reflux of the respiratory stream." Macallum ('84) mentions them in his article on *Amiurus* but ascribes to them no function. Stannius ('39) has described them, as has also Cuvier ('36) who suggests that they not only prevent the reflux of water but the escape of food. Galton ('71), describes the valves and their working in detail, much as Dahlgren ('98) did later. Howes ('83), refers to them in the trout, explaining their function.

In 1898 Dahlgren, who knew nothing of Galton's article,<sup>1</sup> took up the subject in detail and describes the valves in the sunfish, *Eupomotus gibbosus*. The valves are sheets of membrane composed of elastic connective tissue covered with a mucous membrane continuous with that lining the mouth. They are situated in the oral cavity just caudad of the maxillary and mandibular teeth. In this species of sunfish there is a median muscular thickening. The valves "are placed with their edges pointing downward and backward at an angle of less than forty-five degrees to the axis of the body. This angle is increased to about eighty degrees when the valves are struck by the regurgitating stream of water."

The function of the oral valves is to aid in the act of breathing, which has hitherto been described as "a kind of swallowing."

Dahlgren says, "The respiratory stream enters the oral cavity by the mouth and leaves by the two gill openings." . . .

<sup>1</sup> His attention has since been called to it by the present writer.

"In inspiration the stream enters at the mouth in response to a dilation of the oral cavity produced by the outward lateral movement of the opercular frames.

"At the same time water is prevented from entering at the gill openings by the brancheostegal valves which although they are attached to the opercular frames, move independently of and contrary to them; so that, while this outward movement of the frames extends the gill openings, the brancheostegal valves close them automatically by the action of the water which tries to enter.

"In inspiration the water is forced out of the gill openings by a corresponding contraction of the oral cavity. At the same time the water is prevented from regurgitating through the mouth, not by the contraction of the latter, but by the automatic operation of the maxillary and mandibular breathing valves which move as accurately and efficiently as any of the heart's valves. Caught on their posterior edges by the first movement of regurgitation, they snap together and completely prevent the water from leaving the oral cavity by the mouth which, meanwhile, is left partly open, almost as much open as during inspiration.

"That these valves are of value as breathing organs is evident upon casual observation; that they are of much importance is shown by the compensatory action, brought about by injury; that they are not of immediate vital importance is proved by the fishes' ability to get along without their services until they are repaired."

In examining about 70 species of fishes, the writer finds two types of valves. These she has called the crescentic and the U-shaped types. (Fig. 1.) There is a

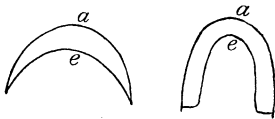


FIG. 1.—Types of valves. C, crescentic; U, u-shaped type. a, attachment; e, free edge.

third form which may, however, be considered as a modification of either type and will be described later.

The crescentic type of valve is typically shown in the catfishes, Siluridae, particularly in *Schilbeodes punctatus*. This type of valve, as its name indicates, is in the form of a crescent with tapering ends, and may be broad or narrow. That of *Eupomotus gibbosus* is also of this type. The

free edge of the crescent is not necessarily a perfect curve (Fig. 2, *a*), but may be interrupted by a projection or a notch. (Fig. 2, *b*, *c*, *d*.)

In the U-shaped type, the ends do not taper but are bluntly truncate. (Fig. 1, *u*.) The free margin in these also may be perfect or interrupted.

A number of interesting modifications occur. As before mentioned, the free edges are often interrupted and in some cases, as in *Pomolobus pseudoharengus* and *Pomolobus æstivalis*, are attached near or at the meson, in one or two lines, to the roof of the oral cavity. (Fig. 3.)

The central thickening which Dahlgren mentions may be a tooth-like projection, may extend only halfway to the free margin or back between the tooth pads, may be straight, wedge-shaped, semi-circular (in this case the flat side was against the attachment), or may be round, this form being either at the meson on

the attachment or in the center of the valve. (Fig. 4.)

In one case, that of *Amciurus natalis*, a horizontal thickening passed through the round centrally situated, mesal thickening. (Fig. 4, *j*.) The thickenings may be found in either or both valves.

They appear to be muscular. Their function may be to strengthen, possibly to tighten, the valves, as they are found on the

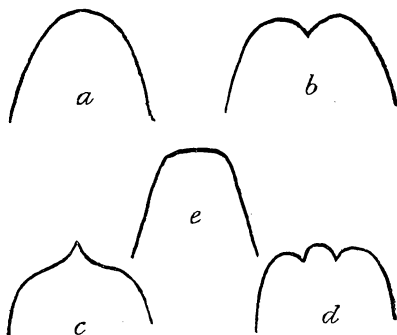


FIG. 2.—Forms of free margin. *a*, perfect; *b*, projection; *c*, notched; *d*, fastened each side of meson; *e*, squared

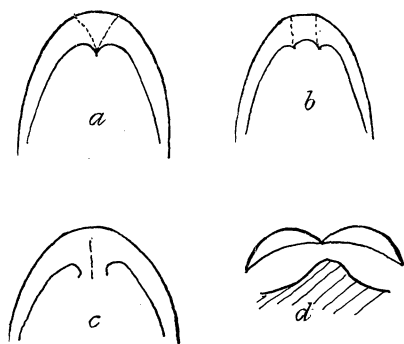


FIG. 3.—Attachment of free edges of maxillary valve at or near meson. *a*, *Clupea pseudoharengus* (v-shaped attachment); *b*, *æstivalis* (parallel attachment); *c*, *Dorosoma* (median linear attachment); *d*, *Astrocopus* (median point attachment).

larger valve when the valves are of unequal size, and this valve

is the more subject to strain and injury from its size and position. What is meant by "position" will be explained in the

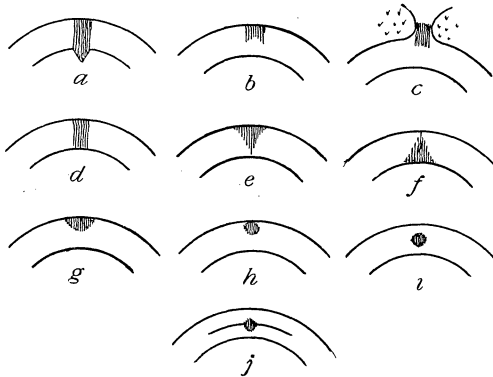


FIG. 4.—Forms of central thickenings. *b*, tooth-pads.

paragraph on the relationship of the valves to the shape of the mouth.

In the majority of species examined, papillæ are found on the valves. These papillæ vary widely in size and arrangement.

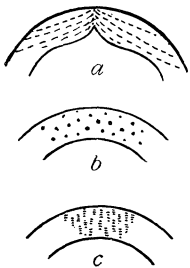


FIG. 5.—Some typical arrangements of papillæ. *a*, in lines; *b*, irregularly scattered; *c*, in short rows so that they resemble a number of small thickenings or folds.

They may be in almost regular rows, scattered, cover the whole valve or only a part of it, even, as in *Cynoscion nebulosus*, run back among the teeth. They may be coarsely setiform, flattened, rounded, on a stalk or, in one case, of a circumvallate appearance. (Figs. 5 and 6.) In some cases the papillæ are fine and closely arranged in rows, giving the appearance of short vertical rows or folds. (Fig. 5*c*.) These are easily distinguished from the true folds found on some valves. These papillæ at first appeared to be one elongated papillus but proved to be as described. In *Ambloplytes gruniens* are found rugæ surmounted by small papillæ.

A third kind of valve has been mentioned as being a modification of either the crescentic or U-type. The writer was for a long time greatly perplexed because many of the Cyprinidæ

apparently had no mandibular valve, yet, from the shape of the mouth, there was every reason to expect a small one. Finally in a large specimen of *Semotilus atromaculatus* it was seen that the place of the valve was taken by several rows of tall papillæ. (Fig. 6, *d*.) This was found to be the condition in all the minnows where the mandibular valve seemed absent.

The function of the papillæ may be to aid in the finding of food. The best development of papillæ seems to be among the bottom feeders, where such sense organs would be most useful. Another modification of the valves is in the pigment which is frequently found in one or both valves. The pigment spots may be regularly arranged or scattered like the papillæ the arrangement varying with the species.

Some valves are further distinguished by rugæ or folds or by

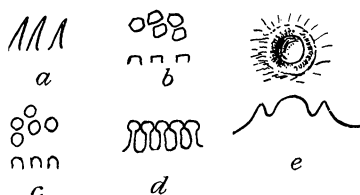


FIG. 6.—Forms of papillæ. *a*, setiform; *b*, vertical section and surface view of the flattened papillæ; *c*, wounded; *d*, stalked, *e*, circumvallate.

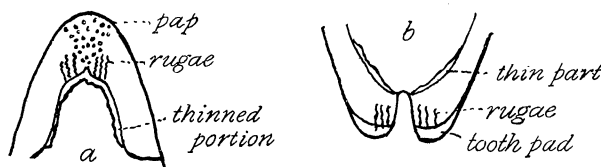


FIG. 7.—Valves of *A. gruniens*. *a*, maxillary; *C*, mandibular.

very thin and transparent margins or both as in the case of *Ambloplytes gruniens* (Fig. 7).

As before stated, the valves are not ever of quite equal size. Their size and shape are dependent on the size and shape of the mouth. For instance, in the case of the Siluridæ, (Fig. 8, *a*) the mouth is terminal, practically horizontal and very wide. For this reason it does not need to be opened far to admit the requisite amount of water, therefore the valves are long and crescentic but only of moderate depth, (*i. e.* the distance from attachment to margin). The mouth being horizontal, the regurgitated stream strikes the two valves with about equal force; therefore, both must be well developed.

In the Catostomidæ, or suckers, the case is very different. Here the mouth is inferior, (Fig. 7, *c*), and the snout depressed. In this family the maxillary valve is well developed and very deep. There are two reasons for this. First, the mouth of the sucker is not wide and must be opened farther; second, the lower valve is entirely absent. The reason for this is obvious. The depressed snout decurves the regurgitated stream, which strikes the upper valve only, hence a lower valve is not necessary, the edge of the upper valve catching against the lower jaw.

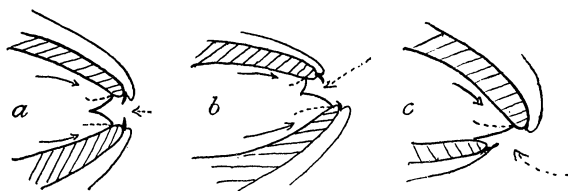


FIG. 8.—*a*, sagittal section showing incurrent and excurrent streams and position of valves when open and closed in horizontal mouth. *b*, similar section in superior mouth; *c*, in inferior mouth.

The position of the maxillary valve in these fishes is nearly horizontal, this being a better position to catch the returning stream. In the case of the minnows whose mandibular valve is replaced by papillæ, and in the case of some other fishes with maxillary valves much larger than the mandibular valves, the mouth is apparently horizontal or even slightly oblique. In all such cases, however, either the snout is depressed or the premaxillary is protractile and is held protracted when the fish is breathing quietly, thus depressing the snout and deflecting the greater part of the water against the maxillary valve.

As may be inferred from the foregoing, the fishes with true oblique mouths possess large mandibular and small maxillary valves. The latter are never completely absent but may be very small. The case of *Astroscoptes y-græcum*, the "stargazer," might be supposed to form an exception to this rule, as the mouth is really superior. From analogy it might be supposed that the maxillary valve would be lacking. Such, however, is not the case. There is a well developed maxillary valve (Fig. 3), like two crescentic valves joined at the meson by their ends.

The reason for this structure is easily seen when the floor of the oral cavity is examined.

This floor is raised in the center and hollowed at each side in such manner as to divide the outgoing stream into two, and the corresponding part of the roof is so shaped and hollowed as to deflect the stream somewhat, so that notwithstanding the superior position of the mouth, the upper valve is necessary.

In *Echensis naucratis*, where the mouth is truly superior, there is a small maxillary valve, whose greatest width is on the parts each side of the meson about half way to the ends. This also can be accounted for by the hollowing out of the roof of the oral cavity.

In *Hemirhamphus unifasciatus* the mouth appears superior, but it is more truly horizontal, the appearance being produced by the great prolongation of the mandible. This species has the maxillary valve but little smaller than the mandibular.

*Pomolobus pseudoharengus* affords a very characteristic example of the development of the mandibular valve. The mouth being very oblique and narrow, the mandibular valve is very deep and "baggy." (Fig. 8.)

In *Chilomycterus schæpfi* the valves are crescentic, the mandibular valve being four times the width of the maxillary valve. The valves are

covered with coarse papillæ. They entirely close the mouth when the jaws are at full stretch, which has been noted in no other species.

A good example of deep valves is found in *Oncorhynchus nerka*, a salmon. In this fish the jaws are hooked, long and somewhat compressed. If the valves were narrow, there would be a long, free margin. Consequently the valves would have to be very heavy to resist the outward pressure from within against the unsupported margins. As it is, the free edges lie far back in the mouth, their length is much reduced and the surface of the valve, which is far better able to stand the strain, increased and hung in a better position for resistance between the bones of the jaws. (Fig. 9.)

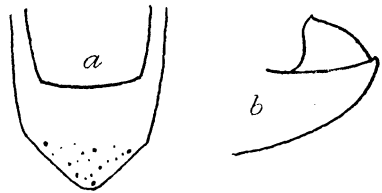


FIG. 8.—Mandibular V of *P. pseudoharengus*. *a*, from above; *b*, from the side.



The valves of predacious fishes seem to be the heavier and more strengthened by muscular thickenings. This may be because the feeding habits of such fish would be liable to injure the more delicate membranes.

The valves vary widely in different genera and in different species of the same genus. The generic variation depends on general shape, size and appearance; the specific on papillæ, muscular thickenings and pigment. The general type of a fam-

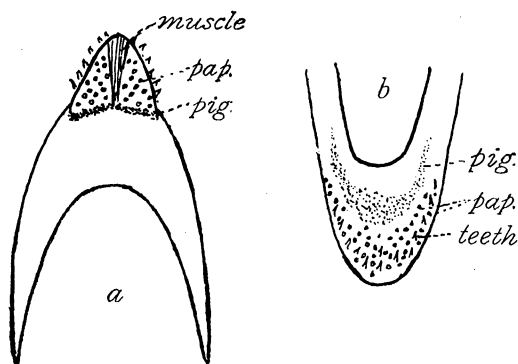


FIG. 9.—Valves of *O. nerka*. *a*, maxillary; *b*, mandibular.

ily, notwithstanding, is very characteristic, except, perhaps in the minnows, in some of which the papillæ form valve occurs. By general type, the general appearance is meant; not the crescentic or U-types only. Individual variation seems comparatively slight and generally resulting from injury. If one individual shows a certain arrangement of pigment, papillæ, and central thickening, it will, so far as it has been possible to ascertain, be found in the rest of the species and nowhere else. For convenience of comparison and explanation the writer has, where enough species and specimens were available, arranged results in synoptical form.

The writer desires to thank Dr. Burt G. Wilder and Dr. H. D. Reed for valuable hints and use of specimens and, more especially, for their kind interest and encouragement.

## CATOSTOMIDÆ.

- A. Papillæ present.
  - B. Small papillæ in fold-like rows over whole valve  
*Erismyzon sucetta*
  - BB. Papillæ not in fold-like rows.
    - C. Papillæ on proximal half <sup>1</sup> of valve *Catostomus macrocheilus*
    - CC. Papillæ over whole valve.
      - D. Papillæ crowded over whole valve; distinct, rounded, not so large as those on lips . . . *Catostomus catostomus*
      - DD. Papillæ less crowded in distal <sup>2</sup> half or in a circular mesal spot.
        - E. Circular mesal spot where papillæ are flattened, small and well separated . . *Catostomus nigriscans*
        - EE. No such spot. Proximal papillæ about size of those on lips and in several rows. Distal papillæ less crowded, flatter, rather elongate  
*Catostomus commersoni*
  - AA. Papillæ absent.
    - F. Small thickenings, perpendicular in direction, resembling long, low papillæ in appearance . . . . *Moxostoma macrolepidotum*

## SILURIDÆ.

- A. Papillæ on both valves.
  - B. Thickenings triangular and in Mand. V.
    - C. Thickening erect-triangular, (apex toward free edge)  
*Amiurus vulgaris*
    - CC. Thickening inverted-triangular, apex toward tooth pads.
      - D. Pigment on thickening and spreading in a crescent through the valve on either side . . *Noturus gyrinus*
      - DD. No pigment in either valve . . . *Noturus miurus*
  - BB. Thickening in Max. V. and not triangular.
    - E. Thickening a vertical rod. Papillæ on Mand. V. larger and closer set than those on Max. V. . . *Amiurus nebulosis*
    - EE. Thickening not a vertical rod.
      - F. Thickening shaped like a sphere with a rod running through it parallel to the free edge  
*Amiurus natalis* (Fig. 4, j.)
      - FF. Thickening spherical, barely touching attachment and covering  $\frac{2}{3}$  the width of the valve. Papillæ so small that the valves at first appear smooth, on proximal  $\frac{2}{3}$  of the Max. V. sparsely scattered on Mand. V.  
*Ictalurus punctatus*

<sup>1</sup> Proximal, — near or toward the attachment.<sup>2</sup> Distal, — away from the attachment.

AA. Papillæ on Mand. V. only.

Central muscular thickening passing between tooth pads

*Noturus flavus*

#### CLUPEIDÆ.

A. Max. V. not attached mesally . . . . . *Clupea harengus*

AA. Max. V. attached mesally.

B. Attached on one perpendicular median line.

C. Mand. V. a crescent, wide; the distal two thirds thin and delicate, no pigment . . . . . *Dorosoma cepedianum*

CC. Mand. V. a horseshoe with pointed ends and the free margin rather squared off at the apex of the curve not perfectly curved like the attachment. Valve much wider at apical part of curve than on sides, (Fig. 2, s)

*Opistheoma oglinum*

BB. Max. V. attached mesally on two lines. (Fig. a. b.)

D. Attachment V-shape. (Fig. 3, a.) *Clupea pseudoharengus*

DD. Attachment in parallel lines, margin between ends of these lines free. (Fig. 3 b.) . . . . . *Clupea æstivalis*

#### PERCADÆ.

A. Thickening in Max. V., a three quarters circle flattened against attachment and covering most of width of valve . . . *Perca americanum*

AA. No thickening.

B. Papillæ and pigment . . . . . *Hadropterus aspro*

BB. No pigment.

C. . . . . *Boleosoma nigrum*

CC. . . . . *Etheostoma caprodes*

#### CENTRARCHIDÆ.

A. Max. V. extending between tooth pads.

B. Papillæ in perpendicular rows on either or both valves.

C. Rows ridge-like (or fold-like).

D. Ridge-like rows on both valves . . *Amblopytes rupestris*

DD. Ridge-like rows on Mand. V. only

Pigment spots on the papillæ . . *Micropterus salmoides*

CC. Papillæ in rows on Mand. V. but not close enough to give ridged appearance. Slight thickenings in V. under the rows of papillæ. Clear margin . . *Eupomotus gibbosus*

BB. Papillæ not in perpendicular rows.

E. Papillæ numerous on one or both valves.

F. Papillæ very large, flat and crowded on both valves, giving tessellated appearance, and extending between tooth pads . . . . . *Apomotus punctatus*

F.F. Papillæ on Max. V. rather flat, medium size, crowded but not giving the appearance of those in F; a few pigment spots at meson; mesal fold *extending but slightly* between tooth pads.

Mand. V. covered with fine rounded papillæ little crowded, pigment in proximal half. . . *E. auritus*

EE. Papillæ few.

G. A few large papillæ on Mand. V. along attachment; central thickening extends through tooth pad and half way to margin; well pigmented. Papillæ in Max. V. fine and well separated

*Chænobrytes gulosus*

GG. No papillæ in Mand. V. Mand. V. well pigmented at base, and meson quite black. Max V. well pigmented, especially between tooth pads. Papillæ few and small . . . . . *Pomoxis sparoides*

AA. Max. V. not extending between tooth-pads.

H. Papillæ in vertical, fold-like rows . . . . . *Apomotus pallidus*

HH. Papillæ not in vertical, fold-like rows.

I. Papillæ of Mand. V. very few and flat, hard to see. Those of Max. V. blunt setiform. Mand. V. well pigmented on proximal half . . . . . *Micropterus dolomieu*

II. Max. V. with fine, rounded, evenly distributed papillæ and slight mesal thickening. Mand. V. with fewer and somewhat larger papillæ; a few pigment spots on base at meson extending through tooth-pads *Eupomotus holbrooki*

#### ARGENTINIDÆ.

Valves crescentic; no papillæ; mandibular valve somewhat the larger.

A. Mesal thickening on mandibular valve circular in shape and placed against attachment of valve, covering about  $\frac{1}{2}$  the width of the valve. Central third of maxillary and proximal half of mandibular valve pigmented . . . . . *Osmerus mordax*

AA. No mesal thickening.

Pigment spots near attachment of mandibular valve, few and variable . . . . . *Hypomesus pretiosus*

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